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Population dynamics and trappability of four rodent species in a forest habitat

by
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Abstract: Trappings were carried out in a forest (*Querco robori-Carpinetum*) habitat on the Dráva Lowlands in two periods, using the capture-mark-recapture method. The sampling grid in the 1 ha study area contained 9 by 9 trap stations for 15 months in 1995-1996, and 11 by 11 stations for 10 months in 1997. A total of 10910 trap nights were recorded in the two periods, during which 71 wood mice (*Apodemus sylvaticus*), 448 yellow-necked wood mice (*Apodemus flavicollis*), 568 striped field mice (*Apodemus agrarius*) and 382 bank voles (*Clethrionomys glareolus*) were marked. Changes in the numbers of rodent populations were characterized using MNA="minimum number alive" and abundance values obtained by the Jolly-Seber estimator. The latter yielded higher values than MNA in the four-trap-night periods and lower values than MNA in the five-trap-night sessions. For the ratio of morning mean number of captures vs. recaptures by species, significantly better results were obtained in the five-night periods.
Key words: live trapping, population dynamics, Jolly-Seber method, trappability, *Apodemus*, *Clethrionomys*

Introduction

Within the framework of the International Biological Programme (IBP) small mammal research played an important role. Besides the main aims of the programme, such as the investigation of the function of small mammals in ecosystems and trophic structures, the analysis of their productivity etc, methodological considerations of trapping were also brought up (Ryszkowski 1969, Hansson 1975, Flowerdew 1976). Several investigations and case studies dealt with the relationship between the size of the trapping grid and the edge effect (Pelikan 1968, 1970, Ryszkowski 1971, Smith *et al.* 1971). Separate studies were devoted to the effect of trapping grid size, which influences density estimations on the one hand (Aulak 1967, Smith *et al.* 1975, Jensen 1975), and is of crucial importance in home range calculations and small mammal movement analysis on the other (Hansson 1969, Zejda & Pelikan 1969, Bondrup-Nielsen 1983).

The technical background of live trapping (trap types, their applicability, effect of baiting, etc.) was a cardinal issue, too. Besides case studies (Kisiel 1972, Dalby & Straney 1976, Maly & Cranford 1985, Getz *et al.* 1986), several earlier and more recent general studies have been published on trapping methodology (Bateman 1971, Gurnell & Flowerdew 1990, Barnett & Dutton 1995). These issues seemed to raise the problem of defining trappability, thus, in addition to formulating estimators for population size and density, trappability was also the subject of scrutiny and several indices have been worked out (Andrzejewski *et al.* 1966, Krebs 1966, Krebs & Boonstra 1984). When evaluating trappability indices, Nichols (1986) suggested the use of maximal trappability estimation. This method of estimation was

also applied by Krebs & Boonstra (1984), and they also assessed the Jolly-trappability and the maximum trappability index defined by Hilborn *et al.* (1976).

Small mammal population studies relying on trapping were started in Hungary in the 1960s (Palotás 1968, 1970). Several research studies were launched in the 1970-80s out of which some focused on small mammal population size estimations (Demeter 1979, 1981), while others intended to analyse correlations between small mammal communities and vegetation cover (Csizmazia 1980, Palotás 1986, Németh 1993). As part of the "Síkfőkut Project", movements of individuals, activity centers and home range sizes were also studied in addition to population dynamics and trophic ecology (Németzki 1984).

Despite the research activity referred to above, Hungarian information on long-term spatial and temporal patterns of small mammals is very scarce. Consequently, monitoring of small mammals in Hungary at the population dynamics level is justified, and it requires multiannual data collection i. e. live trapping in designated sample plots. At the Department of Ecology and Zoogeography in Janus Pannonius University, small mammal live trappings were started in 1994 in a hornbeam-oak forest sample plot in the Dráva Lowlands. In the present study the results from 15 months of four-night trap sampling of four rodent populations and from 10 months of five-night trappings are presented, with focus on population dynamics, capture data and trappability.

Material and methods

Study area

The sampling quadrat is located between the villages of Vajszló and Páprád (N 45 51', E 18 00') in Baranya county, in the Dráva Lowlands. The 1-hectare plot which covers a hornbeam-oak *(Querco robori-Carpinetum)* forest section, is part of the recently designated Bükkhát Forest forest reserve.

Four levels of the vegetation can be differentiated in the grid area. The height of the upper canopy is around 25 m, with a cover of 50-70 %. Characteristic species are *Quercus robur, Fraximus angustifolia* and *Robinia pseudoacacia*. The lower canopy layer is 4–10 m high with 20-95 % cover with the following characteristic species: *Carpinus betulus, Ulmus minor, Fraximus angustifolia* and *Robinia pseudoacacia.* The shrub layer of 1–4 m height and 25–90 % cover consists of young individuals of *Cornus sanguinea, Ligustrum vulgare, Crategus monogyna, Sambucus nigra* and *Robinia pseudoacacia*. Characteristic species of the high herb layer with 90–100 % cover are *Corydalis cava, Anemone nemoralis, Stellaria holostea, Galium aparine, Veronica hederifolia, Lamium purpureum, Alliaria petiolata, Urtica dioica*. In a smaller spot the herb layer is shorter and not very dense (40–70 % cover), and a thick litter of fallen leaves is present. Dominant species are: *Dentaria bulbifera* shoots, *Ficaria verna, Hedera helix, Asperula odorata, Ajuga reptans, Stellaria holostea, Rubus sp.* In patches where the undergrowth is scarce (0-30 % cover) and small, leaf cover is dominant or the surface is bare, with scattered specimens of *Circaea lutetiana, Hedera helix, Pulmonaria officinalis, Asperula odorata*. Since no forestry activity has been carried out in the area for three years, the extent of the latter has decreased parallel with the regeneration of the vegetation.

Trapping methods

In 1995-1996 a 1-ha grid containing 9 by 9 live traps at an equal distance of 12.5 m from each other was used for trapping in the sampling area. Wooden and plastic traps were positioned in the grid points alternately (Horváth *et al.* 1996). Sampling was done in 15 four-night trapping periods from June to October 1995 and from February to November 1996, making up 4860 trap nights. In 1997 the number of nights was raised from 4 to 5, and the grid covering the same 1 ha area contained 121 stations in 11 rows, with traps positioned 10 meters apart. These five-night sampling periods were repeated

monthly from February to November, yielding 6050 trap nights. Thus, the analyses are based on results from a total of 10910 trap nights. Traps were checked twice daily both in 1995-1996 and 1997: starting at 7^{00} CET and 19^{00} CET, totalling 7 and 9 checks, respectively, within one trapping period. Traps were left set up during daytime hours, too. Bacon and whole cereals mixed with vegetable oil or aniseed extract were used as bait.

For individual identification of the animals toe clipping (Begon 1979, O'Farell 1980, Nichols & Conley 1982) was used. When an animal was trapped, its sex, reproductive status, age and weight were recorded.

Variation in population size

Data of the 15 four-night trapping periods in 1995-1996 were recorded in a Manly-Parr diary of captures (Manly & Parr 1968). Temporal changes of population sizes were monitored using the index "minimum number alive" (= MNA) (Petrusewicz & Andrzejewski 1962, Krebs 1966, Boonstra & Krebs 1978).

The modification of the trapping regime in 1998 resulted in an improvement of capture success. Accordingly, the methods of data processing also needed revision: to replace the Manly-Parr capture diary we worked out in Microsoft Access a database system from which queries can be made on capture-histories.

For estimating population size, the Jolly-Seber estimator for open populations was used with help of the JOLLY computer programme (Hines 1988) which runs tests on data using various models in its calculations (Pollock *et al.* 1990). Population size (N_i) was calculated based on the D-model of the programme. This model maintains constant capture probability, a basic criterion of the Jolly-Seber estimator, throughout the study period, and it is reduced in the interpretation of survival probability too, i.e. this parameter is also considered constant by the model. The relative accuracy of the estimation (i.e. coefficient of variation of N: $cv(N)$ (White *et al.* 1982)) was calculated using the standard error of N_i:

$$cv(N) = \frac{SE(N)}{N}$$

The comparison of MNA-trends was made for species-pairs in each period, using Spearman rank-correlation (Zar 1996).

Trappability and daily capture data

Before calculating the trappability index, the trapping success of the two different types of traps was tested. The capture data of wooden and plastic traps were compared in both trapping periods, for each captured species, by the heterogeneity test. Results from the morning samplings in the four-night and five-night periods were compared using the Kruskal-Wallis analysis of variance, based on the ratio of mean number of morning captures and the number of recaptured individuals recorded during the morning samplings.

From the estimated number of marked individuals (M_i), Jolly trappability was calculated (Krebs & Boonstra 1984):

$$Jolly\text{ - }trappability\ (\%) = \frac{\sum_{i=1}^{S} \frac{\Sigma y_i}{M_i} 100}{S}$$

The value M_i is calculated by the JOLLY programme; the number of recaptured animals can be summed for time i from data in the Manly-Parr diary and the database capture history tables (Σy_i). The quotient $\Sigma y_i / M_i$ gives the value of Jolly-trappability based on the i-th sample. Percentage value for

trappability during the whole period is obtained if the sum of these quotients is divided by the number of trapping occasions (S).

Based on the relationship given by Krebs *et al.* (1969), maximum trappability was also calculated (Krebs & Boonstra 1984):

$$maximum-trappability\ (\%) = \sum_{i=1}^{n} \left(\frac{no.\ caught\ in\ sample\ i}{no.\ known\ to\ be\ alive\ in\ sample\ i} \right) 100$$

where n stands for the number of data collections. The relationship between trappability values and population sizes estimated based on the D-model was tested using regression analysis.

Results

Variation in population size

In 1995-96, during the 15 four-night trapping periods 142 yellow-necked wood mice *Apodemus flavicollis* (Melchior 1834), 299 striped field mice *Apodemus agrarius* (Pallas, 1771), 31 wood mice *Apodemus sylvaticus* (Linné, 1758), and 89 bank voles *Clethrionomys glareolus* (Schreber, 1780) were caught and marked individually.

During the five-night samplings between February and November 1997, the distribution of captured and marked individuals of the same four species was as follows: 306 *A. flavicollis*, 269 *A. agrarius*, 40 *A. sylvaticus* and 293 *C. glareolus*. The traps captured also a few specimens of shrews, belonging to the following three species: *Sorex araneus* (Linnaeus, 1758), *Sorex minutus* (Linnaeus, 1766), and *Crocidura leucodon* (Hermann, 1780).

The trends in population size based on capture data from the two periods are depicted by the curves of minimum number alive (MNA) in Figs 1–2. In 1995 the monthly number of captures of *A. agrarius* was higher than those of the other species, and its population increase appearing in September-October exceeded by far that of the other three captured species (Fig. 1). Owing to the long and cold winter in 1995-96 and the following relatively

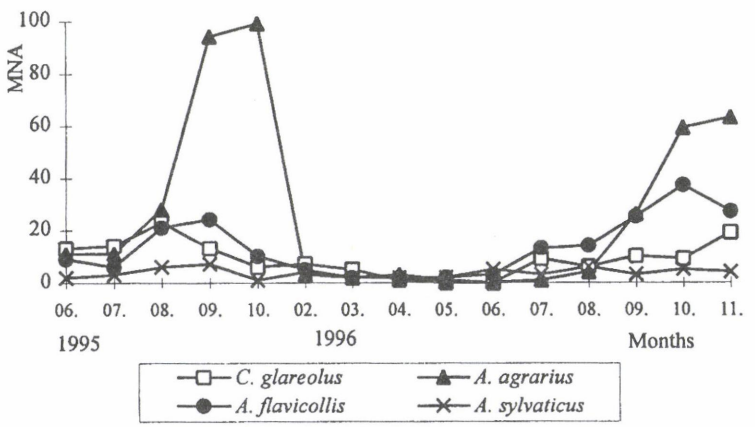

Fig. 1. "Minimum number alive" values of four rodent species in 1995-1996

cold March, rodent populations suffered a serious drop in numbers by spring 1996. The MNA values demonstrate well that in the period before August much fewer individuals were captured than in the previous year, and even the September maxima were lower. *A. agrarius* was the most frequently trapped species in autumn 1996, but with a much lower maximum than in 1995. For this 15-month period significant rank correlation values were obtained in the case of four species-pairs. Changes in numbers were less similar in *A. flavicollis* vs. *A. sylvaticus* ($R_S = 0.55$, $p < 0.05$). The abundance trend of *C. glareolus* was similar to that of *A. agrarius* ($R_S = 0.63$, $p < 0.02$), and identical significance level was shown for the positive correlations between abundances of the pairs *C. glareolus* vs. *A. flavicollis* and *A. agrarius* vs. *A. flavicollis,* respectively (for both: $R_S = 0.67\text{-}0.71$, $p < 0.01$).

In 1997 two abundance maxima could be observed in both *A. flavicollis* and *C. glareolus*, which do not coincide in the two species (Fig. 2). *A. flavicollis* reached its demographic

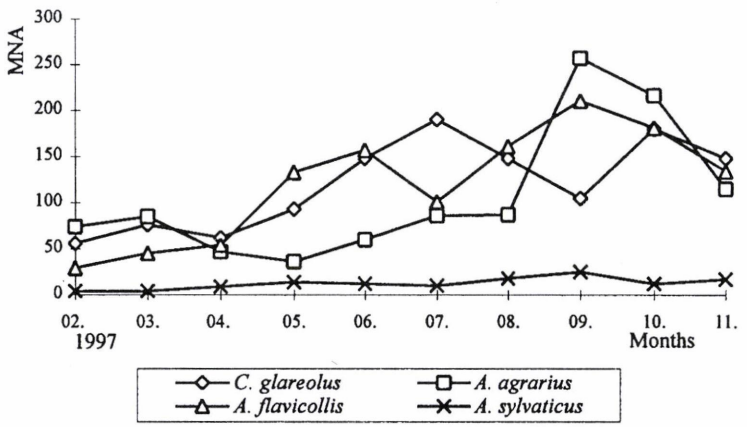

Fig. 2. "Minimum number alive" values of four rodent species in 1997

maximum in May-June and September, while *C. glareolus* was the most abundant in July and October. *A. agrarius* was caught in high numbers in February-March, but by the end of spring its numbers had declined, to increase again only in the autumn to the extent that this species had the highest MNA in September. Throughout the year *A. sylvaticus* was trapped in very low numbers. As revealed by Spearman rank-correlation, population demographic trends of *A. flavicollis* and *A. sylvaticus* were the most similar to each other during this year ($R_S=0.85$, $p < 0.01$). At a lower significance level, the population changes of *A. agrarius* ran nearly synchronously with those of *A. flavicollis* ($R_S=0.64$, $p < 0.05$). As opposed to the 15-month period, no significant rank-correlation values were obtained for the *A. agrarius* vs. *C. glareolus* and the *A. flavicollis* vs. *C. glareolus* species-pairs, which can also be seen on the MNA curves. In cases of higher numbers of *C. glareolus* in the area, the other two species were represented at a low abundance level.

The trend of changes in population sizes estimated for the 1995-1996 period using the D model of the JOLLY programme is similar to the MNA trend, with actual values of the estimation being higher (Fig. 3). The sudden autumn population growth of *A. agrarius* can be clearly seen, which collapses by next spring. However, spring and summer in 1996 did not lead

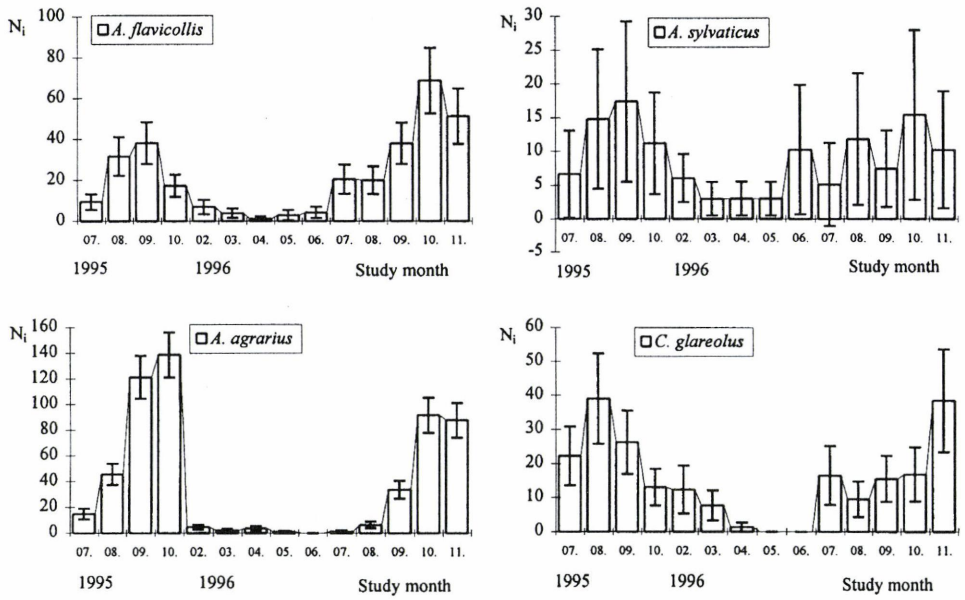

Fig. 3. Population size estimates of four rodent species in 1995-1996, as estimated by the D-model of the JOLLY computer programme (with 95 % confidence interval values shown as bars)

to the demographic decline of this species only: the other three species were also found in very small numbers in the area until August 1996. The rise in population density was late that year, starting only as late as in August, which meant a three-month delay in comparison with the preceding years. This temporal shift of changes in population sizes is well represented by the estimation output values of the D model. The accuracy of the estimation was tested by calculating the coefficient of variation of population sizes (Table 1). Values were not within the limits of acceptability in the case of *A. sylvaticus*, with figures ranging well above 20%.

Table 1. Coefficient of variation (cv[%]) of population size estimates of four rodent species in 1995–1996, based on the D-model

1995-1996/Months	*A. flavicollis*	*A. sylvaticus*	*A. agrarius*	*C. glareolus*
July	20.84	49.47	14.02	19.72
August	15.04	35.47	9.23	17.41
September	13.60	34.77	7.01	18.03
October	15.92	34.16	6.39	21.08
February	25.93	30.08	19.74	29.09
March	29.97	42.38	25	29.16
April	43.90	42.57	25	50.74
May	42.52	42.24	35.08	–
June	32.70	47.41	–	–
July	17.90	61.01	45.6	26.66
August	17.25	41.92	20.96	27.56
September	13.49	38.63	10.37	22.04
October	11.98	41.49	7.67	24.05
November	13.46	43.03	7.78	20.02

The coefficient of variation values in the case of the other three species rose steeply when abundance dropped (in spring and summer 1996 as mentioned above), which indicates that the small number of captures did not allow the Jolly-Seber estimator to be applied successfully for this period. Values estimated by the programme were higher in this period than the MNA figures, meaning that the Jolly-Seber estimator overestimated population sizes in comparison with MNA. If the two parameters are compared monthly using the Wilcoxon test in the case of all four species, the greatest difference between the two data series was obtained for *A. sylvaticus* ($z = 3.29$, $p < 0.001$). Values of the D model estimation were higher than MNA in *A. flavicollis* and *A. agrarius* at $z = 3.17$-3.23, $p < 0.002$, and in *C. glareolus* at $z = 3.05$, $p < 0.003$ significance level.

Many more captures occurred in 1997 than in the preceding years, which can only partly be attributed to the modified sampling regime. Because of the five trap-nights instead of four, and the higher number of traps, population sizes in 1997 cannot, of course, be compared with the results from the previous years. Yet, it can be stated that the higher abundance, which is indicated both by MNA and by D model estimations, is partly a result of the more favourable weather conditions. Population estimations by the D model gave lower values for this year than MNA, except for *A. sylvaticus*. According to these results of the Wilcoxon test, MNA values were higher at the significance level $z = 2.66$, $p < 0.01$ in *A. flavicollis* and *C. glareolus*, while at $z = 2.54$, $p < 0.02$ in *A. agrarius*.

The estimated values also demonstrate the repeated autumn population buildup of *A. agrarius* (Fig. 4). *A. flavicollis* and *C. glareolus* were constantly present in the area at a relatively high abundance, and the asynchrony of their population maxima is reflected in the estimated population sizes, too. The presence of *A. sylvaticus* in much smaller numbers

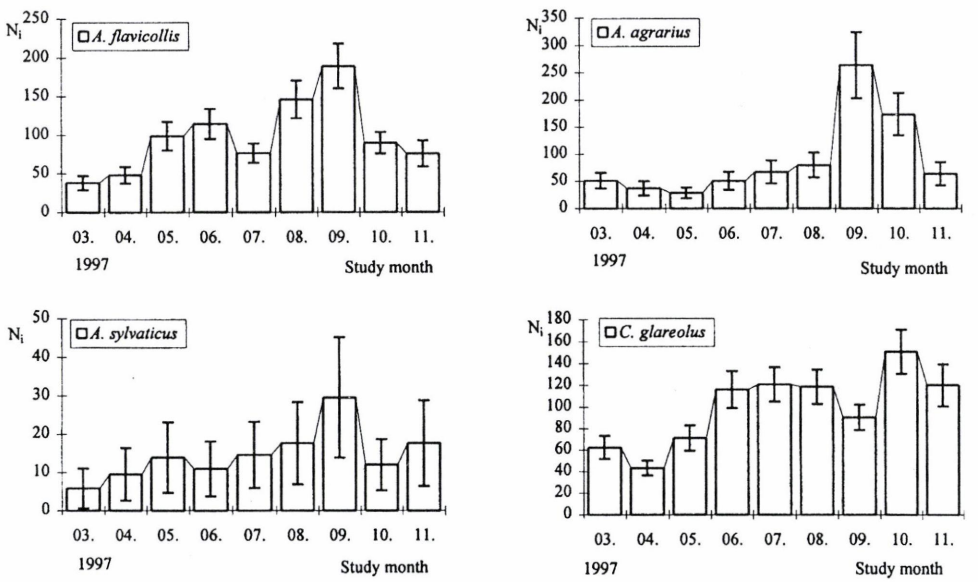

Fig. 4. Population size estimates of four rodent species in 1997, as estimated by the D-model of the JOLLY computer programme (with 95 % confidence interval values shown as bars)

caused the inaccuracy of the estimation that appears in Fig. 5 in the form of wide confidence intervals. The high values of the coefficient of variation (Table 2) in the case of *A. sylvaticus* also suggest the inaccuracy of the population estimates. *A. sylvaticus* with its low capture numbers did not satisfy the conditions of the JOLLY programme, while in the other three species coefficients of variation with values always remaining below 20% are acceptable for each period.

Table 2. Coefficient of variation (cv[%]) of population size estimates of four rodent species in 1997, based on the D-model

1997/Months	*A. flavicollis*	*A. sylvaticus*	*A. agrarius*	*C. glareolus*
March	12.19	45.54	14.37	8.82
April	11.57	36.91	17.80	7.98
May	9.64	33.90	17.41	8.54
June	8.76	33.48	16.69	7.51
July	8.26	30.43	16.12	6.64
August	8.40	31.26	14.44	6.78
September	7.79	27.16	11.67	6.69
October	8.00	28.39	11.51	6.82
November	11.25	32.42	16.95	8.23

Daily capture and trappability

Wooden and plastic traps did not differ significantly in their capture results in either of the trapping periods and in respect of any of the captured species (Tables 3 & 4). Accordingly, the two types of traps operated approximately with identical efficiency in both periods, implying that their mixed use did not cause erroneous sampling.

Table 3. χ^2-test of the trapping capacity of the two trap types in 1995-1996, by species

Species	Number of captures in plastic traps	Number of captures in wooden traps	Total number of captures	χ^2-values	Significance
A. flavicollis	153	126	279	20.85	ns
A. sylvaticus	30	42	72	19.28	ns
A. agrarius	358	284	642	21.69	ns
C. glareolus	85	77	162	8.14	ns

Table 4. χ^2-test of the trapping capacity of the two trap types in 1997, by species

Species	Number of captures in plastic traps	Number of captures in wooden traps	Total number of captures	χ^2-values	Significance
A. flavicollis	553	524	1077	11.75	ns
A. sylvaticus	53	49	102	6.65	ns
A. agrarius	506	481	987	21.3	ns
C. glareolus	440	473	913	8.36	ns

In respect of the mean number of morning captures, no significant difference was revealed by ANOVA (H = 4.97, NS) between the four successive morning samplings, based on the 1995-1996 15-month data series. Comparisons with data of 1997, when each trapping period extended over 5 nights, revealed that the 4th and 5th mornings had a significantly higher value of mean number of morning captures than the 1st and the 2nd (H = 20.22, $p < 0.05$).

The number of morning recaptures was analysed on species basis in both periods. In the 4-night period none of the species exhibited significant variation with respect to the number of morning recaptures recorded during the four successive occasions (H = 3.32-6.64, NS).

No significant difference was revealed by ANOVA between data of the five mornings in 1997 in *A. sylvaticus* and *C. glareolus* (H = 4.45-11.74, NS). In *A. flavicollis* the proportion of recaptures on the 5th morning was significantly higher than on the 1st and the 2nd (H = 16.6, $p < 0.05$), while in *A. agrarius* it was mornings 4 and 5 that were represented with significantly higher recapture values then days 1 and 2 (H = 18.04, $p < 0.05$).

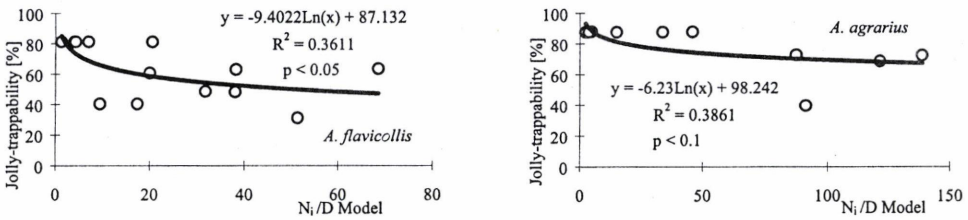

Fig. 5. Jolly-trappability as a function of estimated population size (D-model) in 1995-1996

Values of Jolly trappability in the entire 1995-1996 trapping period were as follows: *A. flavicollis*: 57.4 %, *A. agrarius*: 55.75 %, *A. sylvaticus*: 25.92 %, *C. glareolus*: 45.57 %. Its monthly values were plotted against the population sizes estimated by the D model (Fig. 5) in the case of two species. Negative logarithmic correlation was found at the error level 5% in *A. flavicollis*, and at 10% in *A. agrarius*, which suggests that if the whole period is considered, trappability decreases with increasing population size. However, the early summer interval with low abundance values breaks the trapping period into two terms. If the relationship between trappability and estimated population size is analysed separately for the period starting at the first trapping and lasting until the summer minimum, and for the one lasting from the second half of the summer until the last trapping occassion, it is found that smaller population size values are accompanied by lower trappability. In the autumn period of population buildup trappability values increased with increasing population size, but beyond a certain limit further increase in abundance did not bring about a notable increase in trappability. As data were fewer in the two separate regression analyses of the two shorter periods, negative and positive correlations found for these tendencies were statistically not significant.

Values of maximum trappability in the 1995–1996 period were higher than Jolly trappability, which is in accordance with expectations, since values of the former are influenced by individuals with a single capture and no recapture. For the same reason maximal trappability is given only for the entire period: *A. flavicollis* 80.65 %, *A. agrarius* 76.25 %, *A. sylvaticus* 64.04 %, *C. glareolus* 67.49 %. Due to the lack of sufficient number of recapture data, the correlation between estimated population size and maximum trappability was not analysed.

In the 1997 trapping period Jolly trappability had higher values than the maximum trappability. This is absolutely in contradiction with the former period and our expectations, and it was caused by the fact that the D-model underestimated the number of marked individuals and population sizes in this period, in comparison with MNA. For none of the species was a significant correlation between population size and either of the trappability indices found. Values of Jolly trappability for the entire period are as folows: *A. flavicollis* 69 %, *A. agrarius* 48 %, *A. sylvaticus* 50.18 %, *C. glareolus* 65.24 %, while maximal trappability values are: *A. flavicollis* 37 %, *A. agrarius* 30 %, *A. sylvaticus* 37 %, *C. glareolus* 38 %.

Discussion

The demographic changes of the forest rodent populations in the sampling area during the 15 four-night trapping periods in 1995-1996 and the 10 five-night periods in 1997 were described and presented. The sampling method was not identical in the two periods (difference in trap numbers and the duration of trap operation), thus it is not possible to combine their evaluation.

The dominance of *A. agrarius* at the end of 1995 was shown; in autumn it was trapped in high numbers throughout the sampling area, and its abundance declined early next year. The analysis of population dynamics of *A. agrarius* during this period is reported by Horváth *et al.* (1997), who emphasized the rapid population growth. Earlier studies have also touched upon this characteristic demographic fluctuation of the species (Andrzejewski & Wrocławek 1961, Babiska-Werka *et al.* 1981). Since numbers of other rodent species in the area remained low in comparison with *A. agrarius*, its peaking population in 1995 in the area can be interpreted as one existing in allopatry with the other rodent species. Löfgren (1995) reported on *C. glareolus* allopatry with its dominance in a boreal habitat, in a study showing the niche-expansion of this species in the absence of competitors. Similarly, in our case of *A. agrarius* dominance, competitive relations probably have played an important role. Earlier studies have described the strong dispersal and adaptive capacities of *A. agrarius*, and this species has also been reported as a competitor of *C. glareolus* (Gliwicz 1981).

The marked decrease of populations in 1996 resulted in a distortion of certain calculated parameters. Estimates by the D model of the JOLLY programme were higher in 1996 than the MNA values, while in 1997 they fell below the MNA figures. Nichols & Pollock (1983) pointed out that a condition of the acceptability of MNA method as an estimation is to achieve 100% capture, and the Jolly-Seber estimator usually gives higher values. This was found to be in accordance with our 1995-1996 data, but the opposite situation was experienced in 1997 which fact probably roots in the relation of our 1997 data to the JOLLY programme. The same problem was encountered when calculating the trappability index. Since the JOLLY programme (which considers deaths and accidentally released individuals too) underestimated the number of marked individuals, the value of the Jolly-trappability index had to be smaller than maximal trappability.

According to our results trappability did not depend on the material of the traps: no significant difference was found between the capturing capacity of wooden and plastic traps. The test with different species yielded similar results in this respect.

Only few animals were captured on the first two days of the trapping sessions in the 1995-1996 15 month sampling period. The number of captures rose on the following days of the trappings, with the peak occurring on the 4th day, although the difference between the days

was not significant. This phenomenon can be explained with the adaptation of the animals. In 1997 the trappability of the animals on the first four days of the trappings was again determined by adaptation in that the initially low capture numbers were followed by a sudden increase. Significantly more data were recorded on the 4th and 5th days than on the first two, both in respect of mean number of captures and, in two of the species, in the proportion of recaptures. However, four- and five-night samplings cannot be compared, because in 1995-1996 much fewer traps were used in a grid with different parameters, and a drastic collapse of number of individuals was observed in 1995-1996. Even earlier studies (Begon 1979, Otis *et al.* 1978) suggest a minimum of four nights per period as the criteron for the acceptability of trappping results. When introducing the robust model, Pollock (1982) calculated population sizes using data from five-night periods. Based on our results we also deem five-night trapping periods as more appropriate for small mammal population studies.

Acknowledgements

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